A MORPHOLOGICAL SURVEY ON THE REMARKABLE FLOWER OF *Dillenia indica* (DILLENIACEAE)

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Abstract

Within the flower, the stamens are among the structures that have undergone morphological and functional changes. The pantropical family Dilleniaceae includes ca. 400 species distributed in four subfamilies and 11 genera is among the flowering plants with flowers combining primitive and ancestral structures and poricidal anthers. The aim of this study was to illustrate the general structure of flowers and anthers in *Dillenia indica*. Flower parts are spirally organized including the apocarpous gynoecium composed of 16 to 22 carpels. The androecium has numerous free heterodynamous stamens, spirally organized in several concentric series that can be distinguished in peripherical and central series; the long anthers are poricidal. The ovary is epigynous and polycarpous with many ovules per carpel, axile placentation and anatropous ovules. The sepals persist during development and wrap an indehiscent fruit. All floral whorls are spirally arranged in a Magnoliid-fashion and showed some distinctive characters, such as perianth with persistent sepals that remain attached to the mature fruit; the androecium has at least two types of laminar poricidal stamens which shape is based on the locations (central versus peripherical), and the gynoecium is apocarpous. A mix of basal and derivative state of characters.

Keywords: Heteranthery, Micromorphology, Mosaic evolution, Poricidal anther

Resumo

Os estames estão entre as estruturas florais que sofreram alterações morfológicas e funcionais. Entre as plantas com flores com anteras poricidas, a família pantropical Dilleniaceae inclui cerca de 400 espécies distribuídas em quatro subfamílias e 11 gêneros. O objetivo desse estudo foi ilustrar a estrutura geral das flores, especialmente das anteras em *Dillenia indica*. As partes da flor são organizadas em espiral. O gineceu é apocárpico composto de 16 a 22 carpelos dispostos em espiral. O androceu possui numerosos estames livres, heterodínamos, organizados em espiral em várias séries concêntricas que podem ser distinguidas nas séries periférica e central; as anteras são poricidas. O ovário é epígino e policarpo com muitos óvulos por carpelo, placentação axial e óvulos anátropos. As sépalas persistem durante o desenvolvimento e envolvem o fruto indeiscente. Todos os verticilos florais são dispostos em espiral e apresentam algumas peculiaridades, como o perianto com sépalas persistentes que permanecem presas ao fruto maduro; o androceu tem pelo menos dois tipos de estames laminares poricidas, cuja forma é baseada na localização (central versus periférica), e o gineceu é apocárpico. Há, portanto, uma mistura de estados de caracteres basais e derivados.

Palavras-chave: Anteras poricidas, Evolução em mosaico, Heteranteria, Micromorfologia

Introduction

Approximately 135 million years ago, at the beginning of the Cretaceous, the first plants with specialized reproductive floral structures emerged (FRIIS et al., 2011). Ever since, numerous morphological traits have evolved in association with distinct forms of pollination and insects, often in a coevolutionary relationship favoring dispersal and reproductive success. Within the flower, the stamens are among the structures that have undergone morphological and functional changes. These reproductive organs typically consisting of anther, connective tissue and filament, carry pollen grains containing the male gametophyte. For pollen release to be effective, the anther walls are dehiscent and open so that pollen grains are released, attach to pollinator and are transferred onto the stigma of another flower. According to D´arcy (1996), the anther's functions include pollen production and long-distance dispersal. Stamen and anther shape and structure are

usually adapted to different floral pollination syndromes, thus diversifying the relationship between plants with their biotic pollinating agents.

Anthers can be diversified in several ways: shape, size, and type of dehiscence, which is the splitting of anther with subsequent release of pollen grains (ENDRESS, 1996). Most angiosperms have anthers with longitudinal or transverse slits (ENDRESS & STUMPF, 1991), but other irregular types of dehiscence include valvate and poricidal. Vogel (1978) described three phylogenetic types of flowers with distinct anther position, namely "*Magnolia* type", "*Papaver* type", and "*Solanum* type", as a result of changes in flower shape and anthers over time. According to Bernhardt's (1996) the *Solanum type* is the most derived anther type and dehisces through apical pores, suggesting that poricidal anthers are one of the most advanced forms of anther dehiscence in angiosperms.

Among plant groups with poricidal anthers, the pantropical family Dilleniaceae includes ca. 400 species distributed in four subfamilies and 11 genera (STEVENS, 2019). Its members are characterized by several plesiomorphic characteristics including tall trees with solitary, multi-staminate flowers lacking nectaries, tricolporate pollen, apocarpous gynoecium, follicle or aggregate of follicles fruits (HORN, 2007). Within the family, the genus *Dillenia* L. includes 60 species bearing also basal morphological traits, such as, high number of spirally organized floral structures with apocarpous gynoecium, numerous carpels (16-22) and stamens (~650-850) and terminal idioblasts in leaves (character found in Magnoliaceae) (TUCKER, 1964). These characteristics led some authors to think that Dilleniaceae might be phylogenetically close to the ancestral angiosperm stock (STEBBINS, 1974). However, *D. indica* has flowers with poricidal anthers visited by bees which vibration facilitates the removal of pollen grains, i.e., buzz pollination (BUCHMANN, 1983). In addition, *D. indica* anthers have high amount of pollen and the stamens are arranged in characteristic central and peripherical position suggesting polymorphic heteranthery, a syndrome that involves more than one type of stamen with different function in the same flower (MÜLLER, 1883; VOGEL, 1978; VALLEJO-MARÍN et al., 2010). Most genera (64%) of the Dilleniaceae have anthers exclusively with longitudinal dehiscence, ca. 18% have anthers with longitudinal and poricidal anthers and ca. 18% of the genera have exclusively poricidal anthers (Table 1).

The flowers of *D. inidica* are diurnal but remain open at night. The principal pollinators are bees of various sizes, which remove pollen from the anthers by buzz pollination (ENDRESS, 1997); no nocturnal floral visitors have been reported, but bats are the suspected pollinators in the original environmental species. The flowers have five

tepals and five sepals, but the stamens and carpels are numerous and spirally organized. The androecium is also organized in a spiral fashion. The gynoecium is apocarpous and forms a large multiple yellow fruit with acidic fragrance when ripe

The combination of both advanced and plesiomorphic features is an example of mosaic evolution in this family and may be result of a transformation of anther in relation to pollination selection. Few plant families display the existence of basal and advanced floral characters, which is relatively uncommon in angiosperms, lending this family a good study case for further investigation of floral characters. Within this context, in this study we aim to illustrate the general structure of flowers and anthers in *Dillenia indica*. The specific goals were: 1) to investigate the floral attributes and macro- and micromorphology of the anthers and pollen, and 2) to conduct a literature review to explore the phylogenetic occurrence of poricidal anthers within angiosperms to discuss *D. indica*'s floral characters in relation to the phylogenetic placement of the family within the IV APG scheme.

Material and methods

The study species – D. indica is a tree species naturally distributed from Madagascar and Sri Lanka to Australia and Fiji Islands, but introduced to Brazil as an ornamental tree (HOOGLAND, 1952).

Flowers were collected from four trees at the campus of the Maringá State University, Maringá, Paraná, Brazil, from February to March 2019. The identification of plant material was performed based on taxonomic keys and comparison with specimens cataloged in online databases such as World Checklist of Selected Plant Families (WCSP), The Plant List, Tropicos and the Missouri Botanical Garden. Permanent voucher specimens were deposited at the herbarium HUEM (Herbário da Universidade Estadual de Maringá). For morphological characterization *D. indica* flowers and reproductive structures were fixed in 50% EtOH, formaldehyde, PA 18: 1:1 acetic acid (FAA50) according to Johansen (1940) for at least 48 hours and then preserved in 50% EtOH for further analyses.

Measurement of floral characters – The number of tepals, sepals, carpels, stamen height, width and number were evaluated in ten fresh flowers collected from the four trees. For this, individual floral parts were dissected and arranged in progressive order for assessment. Measurements of height and width of the stamens and every floral structure

sampled were made using a digital caliper. The mean and standard deviation values were calculated with Microsoft Excel®.

Macro- and micromorphology of anthers - The characterization of anthers in *D. indica* was performed using both stereoscope and scanning electron microscopy (SEM). Fresh samples were used for the former and for the latter the floral structures were fixed and preserved in 50% EtOH, then, dehydrated in a graded EtOH series: 70%, 80%, 90%, 100% and 100% for at least 1h on each step. An additional series of dehydration in EtOH/acetone was performed in diluted series as follows: 3:1 for 30 min, 1:1 for 30 min, 1:3 for 30 min, and 100% acetone for 30 min following Almeida et al. (2012). After dehydration the samples were critical point dried in liquid CO_2, sputter coated in gold and examined in SEM Phenom G2. The acquired images were edited using Photoshop CS3. For consistency, both peripherical and central anthers were characterized and described according to their morphological characteristics using at least three samples of each.

Literature review- In order to investigate the occurrence of poricidal anthers in angiosperms, an extensive literature review was performed based on journal articles and online manuscript databases, such as Google Scholar, University of Saskatchewan Library, Scopus, Web of Science, JSTOR, SciELO, Wiley Online Library, ScienceDirect, and Springer. The following key words as topics: poricidal anther, buzz pollination, angiosperms anther, anther, pore was invoked in this search. The anthers considered in this survey were all those that open through a pore, either single apical pore, two apical pores or subapical pores, as described by the authors. The outcome of this search was organized in a taxonomic table including class, family and genera (when available) of taxa reported with poricidal anthers (Table 4). A phylogenetic tree showing the orders with poricidal anthers angiosperms was generated using the online tool Interactive Tree of Life version 1.0 (iTOL®).

Results

Floral characters in Dillenia indica

The species is a tree up to 20 m (Fig. 1A) bearing solitary, terminal, and pendant (hanging as a bell) flowers subtended by a large peduncle developing in the apex of the branch (Fig. 1B). The blossoms are bisexual, actinomorphic and relatively large, measuring approximately 20cm, bowl-shaped and epigynous (Fig. 1C) with delicate

sweet-semi-acidic fragrance. Flower parts are spirally organized and bear a perianth with five flat, oval-oblong to curved petals white-cream and sepals spirally arranged (Figs. 1C, D; 2A, B). The perianth is composed of light green succulent oval sepals that range from 49.2mm to 57.9mm (54.5mm ave.) in length and 44.0mm to 52.6mm (48.0mm ave.) in width (Fig. 2A). The-white caducous petals range from 65.0-91.0 mm (81.6mm ave.) in length and 38.0-53.0mm in width (47.4mm ave.) are also obovate to spatulate in shape (Fig. 2B) (Table 2). The androecium is also organized in spiral fashion and the stamens are arranged in a concentric peripherical and a central series (Figs. 2C-E). The stamens are distinct and the long anther forms a cylindric-tubular structure (Figs. 2C, D). The gynoecium is apocarpous composed of 16 to 22 carpels (19 ave.) spirally arranged (Figs. 2F-I). The stigma lobes are white and smooth and vary from 16 to 22. The ovary is epigynous and polycarpous with many ovules per carpel, axile placentation and anatropous ovules. The sepals persist during development and wrap an indehiscent fruit (Figs. 2J-M).

Nocturnal observations were not performed, but during the day bees were observed, including *Scaptotrigona bipunctata* and *Apis mellifera scutellate*. Both bees collected only pollen grains during the day, but *S. bipunctata* was more active (Fig. 1C). Because the anthers are poricidal and hanging downwards, these bees have no apparent ability to promote buzz pollination or sonication. Thus, the bees use vibration and their jaws to damage the anthers and collect the pollen grains. According to Buchmann (1985) bees adapted to pollen collecting from poricidal anthers are in different families, e.g., Colletidae and Halictidae, among others.

Morphological characterization of androecium and stamens

The androecium has numerous yellow-creamy free stamens spirally organized in several concentric series that can be distinguished in peripherical and central series (Figs. 2C-E); hence, they are heterodynamous. That is, the stamens differ in shape and size and are inserted at different points at the base of the receptacle (Fig. 3A). The stamen insertion is basifixed (Figs. 3A-C). In both central and peripherical stamens, the filament texture has small wrinkles with square-rectangular cell shape on the epidermis (Figs.3D, E). The central stamens are located between the stigmatic lobe spaces (Fig. 2C) surrounding the carpels and vary from 33 to 55 (ave. 47) in number, and measure on average 18.0 mm (16.5-23 mm) in length and 1.9 mm (1-2.45 mm) in width (Table 3). The number of the peripherical is larger than the central stamens and vary from 677 to 862 (ave. 762) and

measure on average 16.2 mm (ranging from 13.2-19.1 mm) in length and 1.0 mm (0.5-1.3 mm) in width.

Macro- and micromorphological characterization of anthers

The two types of anthers in *D. indica* flower are poricidal, with two thecas, and each theca has an apical pore, for a total of two apical pores/anther (Figs. 3A, B) forming a long cylindrical tube that involves nearly two thirds of the anther's length (Fig. 3A). Each of the anther's terminal pore has an operculum (Fig. 3C) that opens to release the pollen. The lateral region of the anther forms a continuous zig-zag pattern, mostly on the adaxial region (Fig. 3B). The anther epidermal surface has irregular-globose cells from the bottom to the top (Figs. 3D, F, G), which a rounded operculum opens on the adaxial surface facing the carpel (Fig. 3C). The filament cells in also irregular, with a rectangular shape (Figs. 3D, E). Both the central and peripherical anthers are typically loaded with small pollen grains of ca. 20-30µm in diameter (Figs. 4A-C). In central anthers, most pollen grains are spheric and tricolpate with pores and micropores of irregular shape on the surface (Figs. A, B). In peripherical anthers, the pollen is also spherical (Figs. 4C-F), along with some irregular pollen grains of oval (Fig. 4D), pentagonal (Fig. 4E), square (Fig. 4F) and other unusual irregular shapes was observed.

Phylogenetic occurrence of poricidal anthers in angiosperms

Poricidal anthers occur in 21 orders of flowering plants including monocots (Alismatales, Asparagales, Commelinales, Poales) and eudicotyledons (Apiales, Boraginales, Caryophyllales, Cucurbitales, Dilleniales, Ericales, Fabales, Gentianales, Lamiales, Malpighiales, Malvales, Myrtales, Oxalidales, Rosales, Santalales, Solanales and Zygophyllales) (Fig. 5).

According to APG's (2001) phylogenetic tree, poricidal anthers were found in four monocotyledonous orders, eight rosids, six asterids and three uncertain groups in the angiosperm phylogenetic tree, among them: Dilleniales, Santalales and Caryophyllales. In total, 50 families have at least one species with a poricidal anther, grouping 166 genera (Table 4). The order Ericales accounts 35% of the poricidal anther genera, followed by Malpighiales with 14%, accounting together almost 50% of poricidal anthers genera.

Discussion

The vegetative and morphological features of *D. indica* are quite characteristic and encompass an amalgamation of plesiomorphic and advanced characters. The large and scented hermaphrodite flower in particular has special attributes. All floral whorls are spirally arranged in a Magnoliid-fashion and showed some peculiarities, such as the perianth with persistent sepals that remain attached to the mature fruit; the androecium has at least two types of laminar poricidal stamens which shape is based on the locations (central versus peripherical), and the gynoecium is apocarpous. A mix of basal and derivative state of characters.

Stamen dimorphism and deviations from typical stamen morphology, including anther diversity, size, and shape, have intrigued scientists for many years. Darwin (1899) suspected that stamens related to heteranthery had different functions but was unable to understand their roles. Lloyd (2000) discussed the "feeding" anthers, which producs "feed pollen." Usually, plants that have flowers with this kind of anther are nectarless and the main floral reward is pollen. The difference between central and peripherical anthers in *D. indica* offer the possibility of different pollen types, potentially a "feeding pollen," that is pollen grains with the necessary proteins, fats and carbohydrates. Even with the lack in the studies regarding pollen viability, it is possible that in some peripherical anthers the pollen grains are "cheap" and not necessarily nutritious and/or not reproductively viable. Some pollen analyzes regarding Dilleniaceae, e.g., Furness (2007), Furness & Rudall (2004), reported that in *Tetracera* spp., pollen grains are inaperturate, just like some found in peripherical anthers of *D. indica*; however, it was not noticed any other morphological difference (size, shape or epidermal wall sculpturing) between triporate and inaperturate grains. Therefore, as Anderson & Symon (1989) discussed, it is probable that the peripherical anther's pollen is a reward to pollinators, such as in some *Solanum* L. flowers. However, studies regarding the difference between introduced plants and native plants could be interesting to compare both peripherical anther's pollens to confirm whether there is a difference between pollen in peripherical and central anther in the natural environmental. Also, a survey regarding both peripherical and central pollen's viability would be interesting to better understand *D. indica*'s pollination system.

According to Vallejo-Marín et al. (2010), heteranthery is highly linked to poricidal anthers, whose mechanisms may be related to the reduction of pollen consumption by floral visitors, leaving more pollen for pollination. However, *A. mellifera* and *S. bipunctata* are not bees recognized for buzz pollination; nevertheless, small

disruptions in their surface were observed throughout the stamen, indicating a possible pollen “theft” for food functions. Endress (1997) observed many floral visitors in *D. indica*, *D. philippinensis* and *D. suffruticosa*, and *Xylocopa* sp. was considered an efficient pollinator. According to the author, these bees grab many poricidal anther stamens and vibrate their thorax, agitating the anthers and releasing the pollen grains. Then, the bee gathers another group of stamens and repeat the action so that it can transfer the pollen wedged in their body and to the stigmata lobe.

Although there are some floral visitors reports to *Dillenia* sp. flowers, there are almost no references regarding their pollinators. Corner (1988) mentions bees, small beetles and flies as likely pollinators. In general, its floral visitors are considered apiforms, among them *Xylocopa* sp., but often small bees, which are not probable pollinators (BURKILL, 1916; 1919) such as *Bombus morio* (AMARAL NETO, 2011) and *A. mellifera* (NOWICKE & MESELSON, 1984).

Because of the lightweight of pollen grains and the wide opening of the flower during anthesis, there is the possibility that anemophily might be the legitim pollen transport agent of specie. The evolution of anemophily is often explained regarding the environmental variation, caused by typical weather or the evolution of earth climate in the past million years (CULLEY et al., 2002). Although it is considered difficult for poricidal anthers to release pollen, *D. indica*’s pollen quantity is very large and can be released with a simple hand touch. In addition, according to Culley et al. (2002), *D. indica* has some traits typically associated with wind and biotic pollination, such as pollen size, number of pollen and absent nectary. It may indicate a different pollination syndrome depending on whether the specimens are in a native or introduced environment.

The first approach for the taxonomic revision of poricidal anthers was made by Harris (1905), whose apical dehiscence stamens were divided into 7 types. Later, Buchmann (1978) revived Harris's poricidal anthers classification, but with the addition of the buzz pollination, grouping a total of 72 families. However, the complete list of plants with poricidal terminal openings in Buchmann (1978) presents unconventional orders, such as Laurales, Canellales and Liliales, known for valvar or filamentous anthers. It happened because Buchmann considered poricidal anthers the species whose has short apical slits, short transverse slits, valves or legitim apical pores.

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Table 1. Type of anther dehiscence in Dilleniaceae. Taxonomic arrangement follows Horn (2007).

Subfamily	Genera and (#spp)	Anther dehiscence	Reference
Delimoideae	*Tetracera* (50)	Longitudinal	Hoogland (1953)
Dillenioideae	*Acrotrema* (9)	Poricidal	Dickison (1971)
	Dillenia (65)	Poricidal and Longitudinal	Hoogland (1952)
	Didesmandra (1)	Longitudinal	Dickison (1970)
	Schumacheria (3)	Poricidal	Dickison (1970)
Doliocarpodeae	*Curatella* (1)	Longitudinal	Kubitzki (1971)
	Davilla (25)	Longitudinal	Kubitzki (1971)
	Doliocarpus (45)	Longitudinal	Kubitzki (1971)
	Neodillenia (2)	Longitudinal	Aymard (1997)
	Pinzona (1)	Longitudinal	Kubitzki (1971)
Hibbertioideae	*Hibbertia* (225)	Poricidal and Longitudinal	Dickison (1970)

Table 2. Floral morphological characteristics of *D. indica*. Perianth and gynoecium morphometrics data was made using the same flowers used in Table 3.

Whorl/Organ	Character	
Perianth		
Sepals	Shape and margin	Oval, entire
	Color	Light green
	Number	5
Petals	Shape and margin	Elongated, entire
	Color	White
	Number	5
Androecium		
Central stamen	Attachment	Basifixed
	Dehiscence	Poricidal
	Number	~47
	Height	~16mm
	Width	~1mm
Peripherical stamen	Type	Basifixed
	Dehiscence	Poricidal
	Number	~841
	Height	~19mm
	Width	~1.9mm
Gynoecium		
Carpel	Number	Multicarpelar (~19)
Locule	Number	Multilocular (~19)
Ovary	Position	Epigynous
	Placentation	Axilar
Ovule	Attachment	Anatropous
	Number	~50 per carpel (~950 in total)

Table 3. Androecial characters of *Dillenia indica*. Sample size (n = 10)

Flower Number	#Central stamens	Height central stamens (mm)	Width central stamens (mm)	#Peripherical stamens	Height peripherical stamens (mm)	Width peripherical stamens (mm)
1	33	23.0	1.0	710	15.0	0.5
2	33	23.0	1.0	706	15.0	0.5
3	55	17.5	1.9	862	13.1	1.2
4	54	16.5	2.1	790	15.9	0.8
5	49	16.7	2.4	850	15.8	0.7
6	50	18.9	2.1	650	17.9	1.0
7	48	16.7	2.1	760	16.7	1.0
8	53	18.9	2.2	834	16.0	1.2
9	44	17.6	2.2	677	19.0	1.2
10	47	18.0	1.7	781	15.5	1.3
$\bar{x}$	47(±7.5)	18.7(±2.3)	1.9(±0.5)	762(±70.4)	16.2(±1.5)	1.0(±0.3)

Table 4. Taxonomic occurrence of poricidal anthers in angiosperms

Order	Family	Genus	Reference
Alismatales	Araceae		Buchmann, 1983
		Culcasia	French, 1985
		Lagenandra	Grayum, 1990
		Cryptocoryne	Grayum, 1990
Asparagales	Tecophilaeaceae		Harris, 1905
		Conanthera	Harris, 1905
		Cyanastrum	Brummitt et al., 1998
		Cyanella	Harris, 1905
		Tecophilea	Harris, 1905
		Walleria	Carter, 1962
		Zephyra	Harris, 1905
Poales	Poaceae		Knuth & Loew 1899
		Dichanthium	Bano et al., 2008
	Rapateaceae		Harris, 1905
		Cephalostemon	Harris, 1905
		Rapatea	Harris, 1905
		Saxofridericia	Harris, 1905
		Schoenocephalium	Harris, 1905
		Spathathus	Harris, 1905
		Stegolepis	Harris, 1905
Commelinales	Commelinaceae		Harris, 1905
		Cartonema	Harris, 1905
		Dichorisandra	Harris, 1905
	Haemodoraceae		Buchmann, 1983
		Conanthera	Simpson, 1990
		Cyanella	Simpson, 1990
		Odontostomum	Simpson, 1990
		Tecophilaea	Simpson, 1990
		Zephyra	Simpson, 1990
Dilleniales	Dilleniaceae		Harris, 1905
		Acrotrema	Dickison, 1971
		Dillenia	Hoogland, 1952
		Hibbertia	Dickison, 1971
		Schumacheria	Dickison, 1971
Zygophyllales	Krameriaceae		Buchmann, 1983
		Krameria	Harris, 1905
Oxalidales	Elaeocarpaceae		Buchmann, 1983
		Tetratheca	Downing et al., 2008
		Tremandra	Downing et al., 2008
Malpighiales	Achariaceae		Harris, 1905 (Flacourtiaceae)
		Kiggelaria	Harris, 1905 (Flacourtiaceae)
	Euphorbiaceae		Buchmann, 1983
		Euphorbia	Islam et al., 2008
	Malpighiaceae		Vogel, 1978
		Janusia	Anderson, 1987
		Tristellateia	Anderson, 1987
	Ochnaceae		Harris, 1905;
		Blastemanthus	Buchmann, 1978
		Brackenridgea	Buchmann, 1978
		Cespedesia	Amaral & Bittrich, 2014
		Elvasia	Amaral & Bittrich, 2014
		Euthemis	Buchmann, 1978
		Fleurydora	Amaral & Bittrich, 2014
		Godoya	Amaral & Bittrich, 2014
		Krukoviella	Amaral & Bittrich, 2014
		Lavradia	Buchmann, 1978
		Lophira	Amaral & Bittrich, 2014

		Luxemburgia	Amaral & Bittrich, 2014
		Ochna	Buchmann, 1978
		Perissocarpa	Amaral & Bittrich, 2014
		Poecilandra	Buchmann, 1978
		Rhytidanthera	Amaral & Bittrich, 2014
		Sauvagesia	Buchmann, 1978
		Ouratea	Vogel, 1978
	Phyllanthaceae		Vorontsova & Hoffmann, 2008
		Poranthera	Vorontsova & Hoffmann, 2008
	Rafflesiaceae		Buchmann, 1983
		Rafflesia	Barcelona et al., 2009
Fabales	Leguminosae		Harris, 1905
		Cassia	Harris, 1905
		Chamaecrista	Tucker, 1996
		Dicorynia	Harris, 1905
		Distemonanthus	Harris, 1905
		Koompassia	Harris, 1905
		Labichea	Harris, 1905
		Storckiella	Harris, 1905
	Polygalaceae		Venkatesh, 1956;
		Polygala	Venkatesh, 1956;
Rosales	Cannabaceae		Knuth & Loew 1899
		Humulus	Xu & Deng, 2017
Cucurbitales	Begoniaceae		Harris, 1905
		Begonia	Harris, 1905
Myrtales	Melastomataceae		Harter et al., 2015;
		Comolia	Mesquita-Neto et al., 2018
		Lavousiera	Mesquita-Neto et al., 2018
		Leandra	Harter et al., 2015
		Macairea	Mesquita-Neto et al., 2018
		Miconia	Mesquita-Neto et al., 2018
		Pterolepis	Mesquita-Neto et al., 2018
		Rhynchanthera	Harter et al., 2015
		Tibouchina	Harter et al., 2015
	Myrtaceae		Buchmann, 1983
		Babingtonia	Wilson et al., 2001
		Beaufortia	Wilson, 2010
		Darwinia	Wilson et al., 2001
		Eucalyptus	Beardsell et al., 1993;
		Regelia	Wilson, 2010
		Verticordia	Ladd et al., 1999
Malvales	Cochlospermaceae		Buchmann, 1983
		Amoreuxia	Johnson-Fulton et al., 2017
		Cochlosperinum	Keating, 1972
	Dipterocarpaceae		Harris, 1905
		Monoporandra	Harris, 1905
		Stemonoporus	Harris, 1905
	Malvaceae		Harris, 1905
		Guichenotia	Harris, 1905
		Lasiopetalum	Harris, 1905
		Thomasia	Harris, 1905
Santalales	Misodendraceae		Buchmann, 1983
		Misodendrum	Kuijt & Hansen 2015a
	Olacaceae		Buchmann, 1983
		Anacolosa	Malécot et al., 2004
		Aptandra	Malécot et al., 2004
		Cathedra	Malécot et al., 2004
		Chaunochiton	Malécot et al., 2004
		Ongokea	Malécot et al., 2004
		Phanerodiscus	Malécot et al., 2004

	Santalaceae		Buchmann, 1983 (alterado)
		Korthalsella	Kuijt & Hansen (2015b)
Caryophyllales	Halophytaceae		Pozner & Cocucci, 2006
		Halophytum	Pozner & Cocucci, 2006
Ericales	Actinidiaceae		Buchmann, 1983
		Actinida	Keller et al., 1996
		Clematoclethra	Keller et al., 1996
		Saurauia	Keller & Breedlove, 1981
	Clethraceae		Buchmann, 1983
		Clethra	Schönenberger et al.,2012
	Cyrillaceae		Buchmann, 1983
		Purdiaea	Thomas, 1960
	Ebenaceae		Buchmann, 1983
		Diospyros	Hiern, 1873
	Ericaceae		Buchmann, 1978
		Agapetes	Buchmann, 1978
		Agauria	Buchmann, 1978
		Andromeda	Buchmann, 1978
		Arbutus	Buchmann, 1978
		Arctostaphylos	Buchmann, 1978
		Bejaria	Stevens et al., 2004
		Ceratostema	Stevens et al., 2004
		Chamaedaphne	Stevens et al., 2004
		Costera	Stevens et al., 2004
		Demosthenesia	Stevens et al., 2004
		Dimorphanthera	Stevens et al., 2004
		Diogenesia	Stevens et al., 2004
		Disterigma	Stevens et al., 2004
		Gaylussacia	Stevens et al., 2004
		Kalmia	Stevens et al., 2004
		Monotropsis	Stevens et al., 2004
		Oreanthes	Stevens et al., 2004
		Pellegrini	Stevens et al., 2004
		Rhododendron	Buchmann, 1978
		Rhodothamnus	Buchmann, 1978
		Satyria	Stevens et al., 2004
		Semiramisia	Stevens et al., 2004
		Symphysia	Stevens et al., 2004
		Vaccinium	Buchmann, 1978
	Lecythidaceae		Buchmann, 1978
		Allantoma	Buchmann, 1978
		Asteranthos	Buchmann, 1978
		Barringtonia	Buchmann, 1978
		Bertholletia	Buchmann, 1978
		Cariniana	Buchmann, 1978
		Corythophora	Buchmann, 1978
		Couratari	Buchmann, 1978
		Eschweilera	Buchmann, 1978
		Grias	Buchmann, 1978
		Gustavia	Buchmann, 1978
		Lecythis	Buchmann, 1978
	Myrsinaceae		Harris, 1905
		Ardisia	Ståhl & Anderberg 2004
		Cybianthus	Ståhl & Anderberg 2004
		Monoporus	Ståhl & Anderberg 2004
		Tapeinosperma	Ståhl & Anderberg 2004
		Yunckeria	Ståhl & Anderberg 2004
	Pentaphylacaceae		Buchmann, 1983
		Pentaphylax	Van Steenis 1955
	Primulaceae		Buchmann, 1983

		Cyclamen	Affre & Thompson 1997
		Dodecatheon	Harder & Barclay, 1994
	Pyrolaceae		Buchmann, 1978
		Chimaphila	Buchmann, 1978
		Moneses	Buchmann, 1978
		Orthilia	Knudsen & Oleson, 1993
		Pyrola	Buchmann, 1978
	Sarraceniaceae		Keller et al., 1996
		Heliamphora	Kubitzki 2004
	Sladeniaceae		Buchmann, 1983
		Ficalhoa	Luna & Ochoterena, 2004
		Sladenia	Stevens & Weitzman, 2004
Gentianales	Gentianaceae		Harris, 1905
		Cotylanthera	Struwe & Pringle, 2018
		Exacum	Struwe & Pringle, 2018
		Orphium	Struwe & Pringle, 2018
	Loganiaceae		Harris, 1905
		Gardneria	Harris, 1905
	Rubiaceae		Buchmann, 1983
		Argostemma	Harris, 1905;
		Strumpfta	Harris, 1905;
Solanales	Solanaceae		Harris, 1905
		Cyphomandra	Harris, 1905
		Solanum	Harris, 1905
Boraginales	Boraginaceae		Buchmann, 1983
		Halgania	Holstein & Gottschling, 2018
Lamiales	Acanthaceae		Buchmann, 1983
		Mendoncia	Schönenberger & Endress, 1998
		Pseudocalyx	Schönenberger & Endress, 1998
	Byblidaceae		Buchmann, 1983
		Byblis	Conran & Carolin (2004)
	Gesneriaceae		Harder & Barclay, 1994
		Beccarinda	Weber 2004
		Leptoboea	Weber 2004
	Pedaliaceae		Islam et al., 2008
		Pedalium	Islam et al., 2008
Apiales	Pittosporaceae		Buchmann, 1983
		Billardiera	Harris, 1905
		Cheiranthera	Carolin & Bittrich 2018

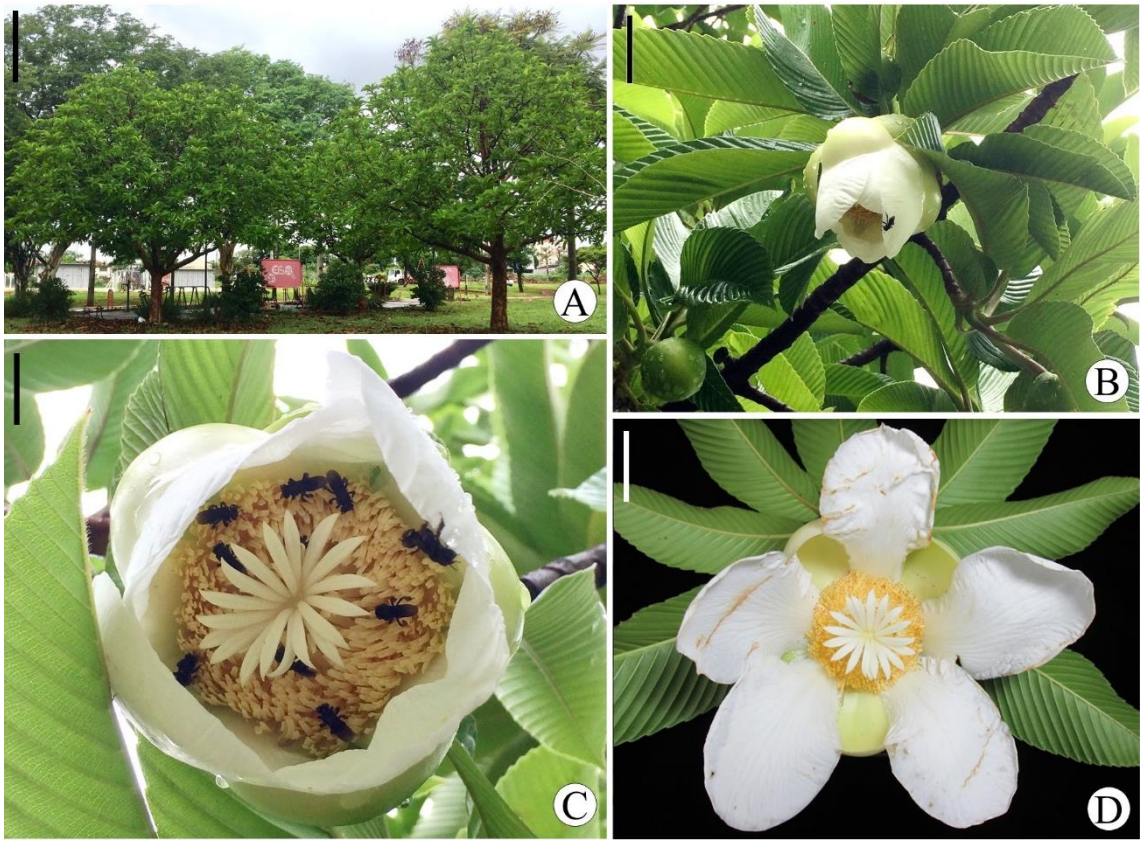


Figure 1. Representative features of *Dillenia indica*. A: Individual trees cultivated at the campus of the Universidade Estadual de Maringá, Brazil. B: Pendulous terminal flower attached to tree; C: Hermaphrodite flower in early anthesis with visiting *Scaptotrigona bipunctata*; D: Flower showing five petals in late anthesis. Scale bars A: 2m; B: 10cm; C: 3cm; D: 6cm.

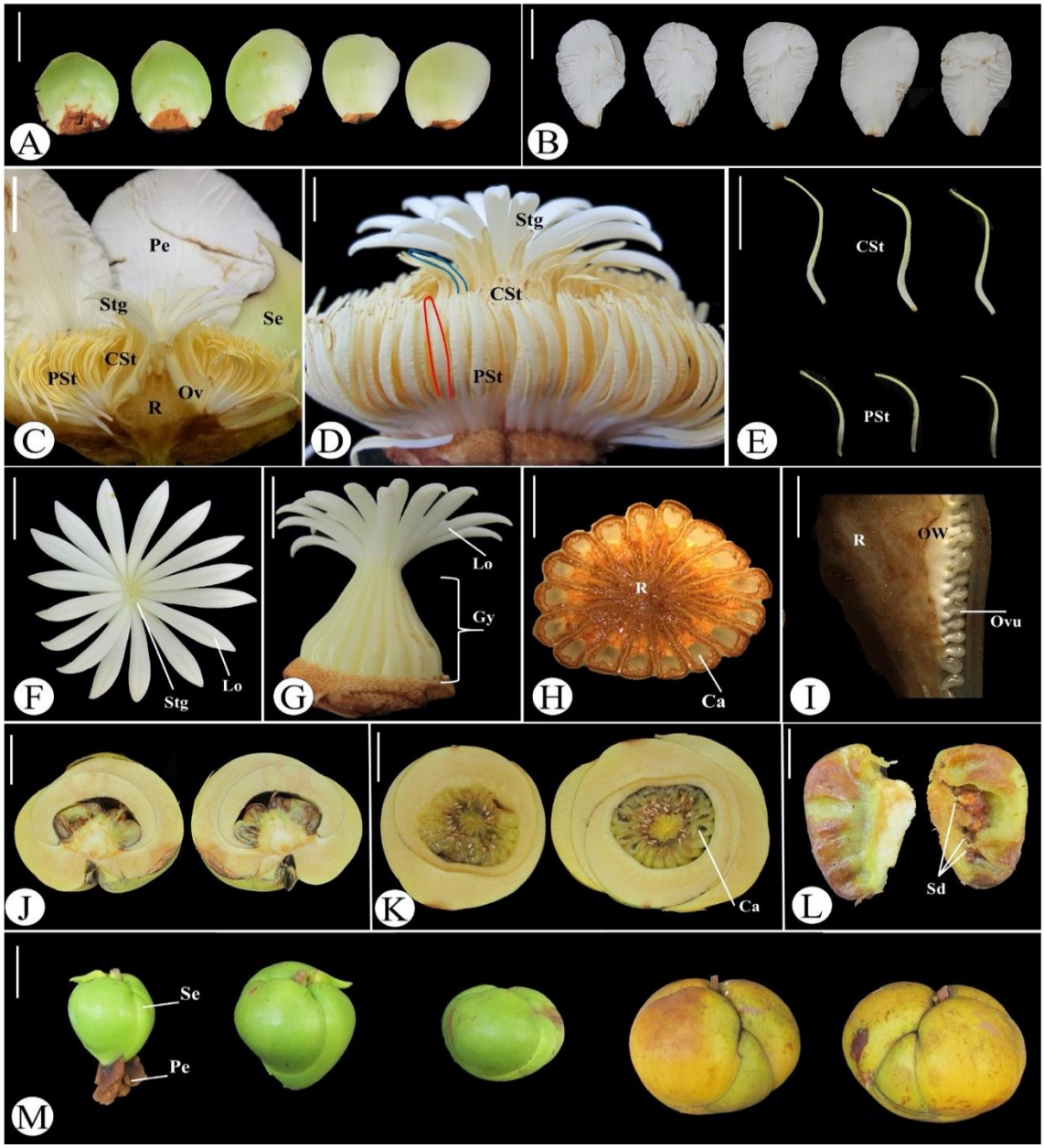


Figure 2. Floral and fruit attributes in *Dillenia indica*. A: Oblong to ovate sepals; B: Obovate to spatulate petals; C: Longitudinal section of the flower showing parts of the perianth, androecium and gynoecium; D: Flower with perianth removed displaying androecium with peripherical (red outline) and central (blue outline) laminar stamens and gynoecium with multiple lobes in the stigma; E: Central (above) and peripherical (below) stamens; F: Close-up of stigma and lobes; G: Gynoecium showing ovary, style and stigma lobes; H: Cross section of multicarpelate ovary and receptacle; I: Longitudinal section of the ovary and ovules; J: Fruit in longitudinal section K: Fruit in and cross section; L: Fruit with seeds; M: Developmental series of the indehiscent fruit. Ca: Carpel; CSt: Central Stamen; Gy: Gynoecium; Lo: Lobe; Ov: Ovary; Ovu: Ovule; OW: Ovary Wall; Pe: Petal; PSt: Peripherical stamen; R: Receptacle Sd: Seed; Se: Sepal; Stg: Stigma. Scale bars A: 5cm; B: 2cm; C: 1cm; D: 0.3cm; E: 3cm.

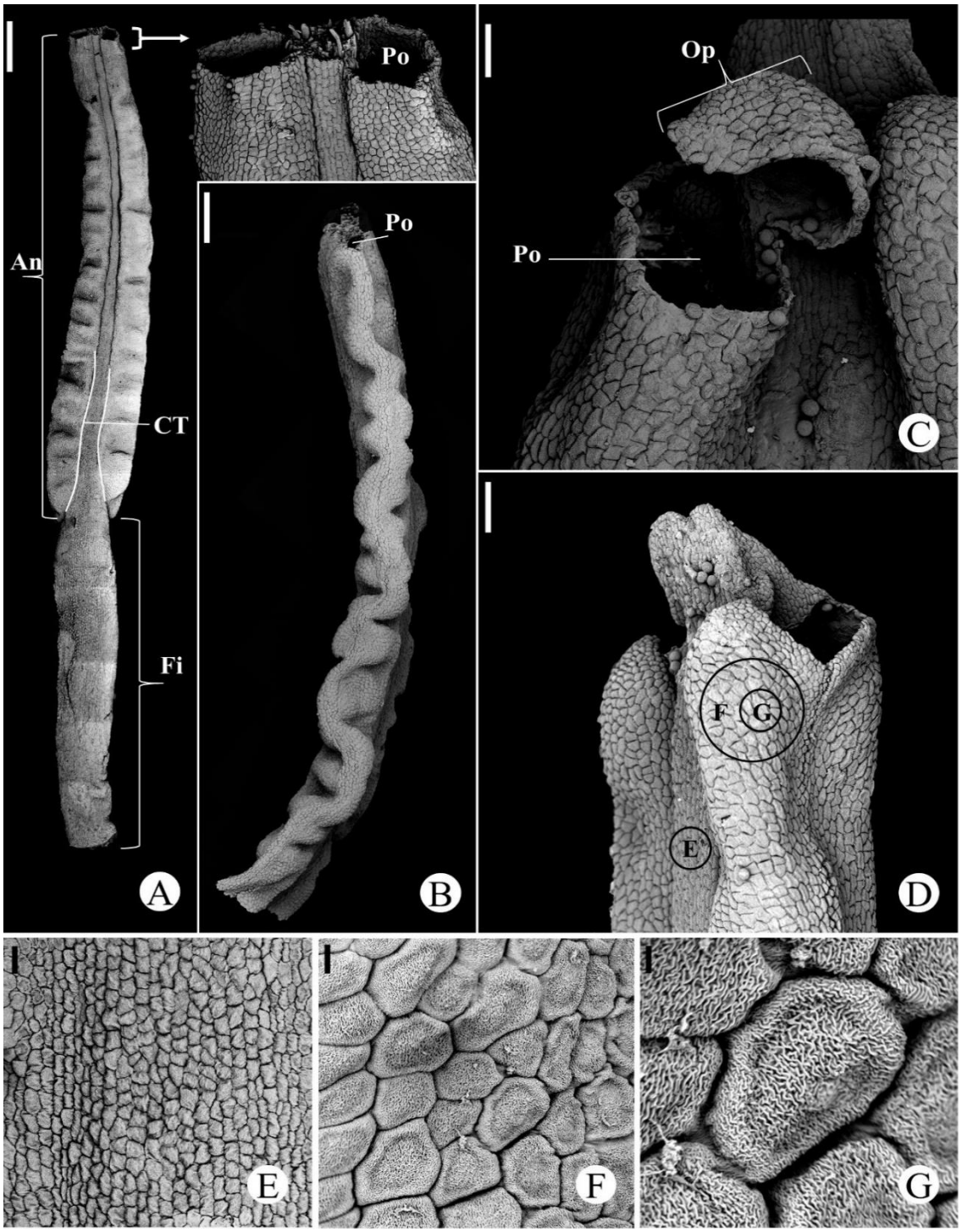


Figure 3. Macro- and micromorphology of stamens in *Dillenia indica*. A: Peripherical laminar stamen with poricidal anther and arrow pointing to the pore magnification; B: Lateral view of zig-zagged central stamen; C: Poricidal anther with operculum in central stamen; D: Pore opening of central anther; E-G: close-up of epidermal cells in anthers as indicated by circles in D. F: Anther cells; G: Cell texture detail. An: Anther; CT: Connective tissue; Fi: Filament; Po: Pore. Scale bars A: 740µm; B: 300µm; C: 120µm; D: 90µm; E: 55µm; F: 15µm; G: 5µm

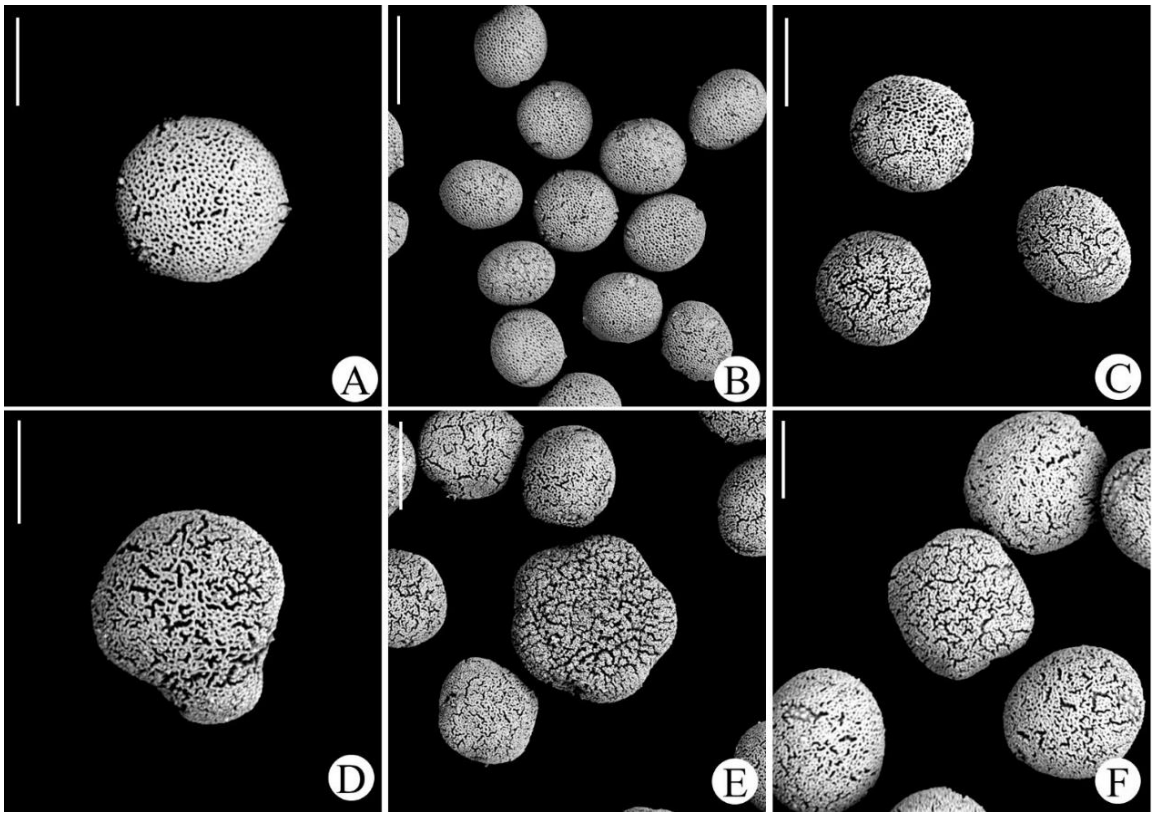


Figure 4. Different pollen types in peripherical and central anthers of *Dillenia indica*. A-B. Tricolpate pollen from central anthers. C-F. Tricolpate pollen from peripherical anthers. Scale bars A: 5µm; B: 20µm; C: 15µm; D: 10µm; E: 15µm; F: 10µm

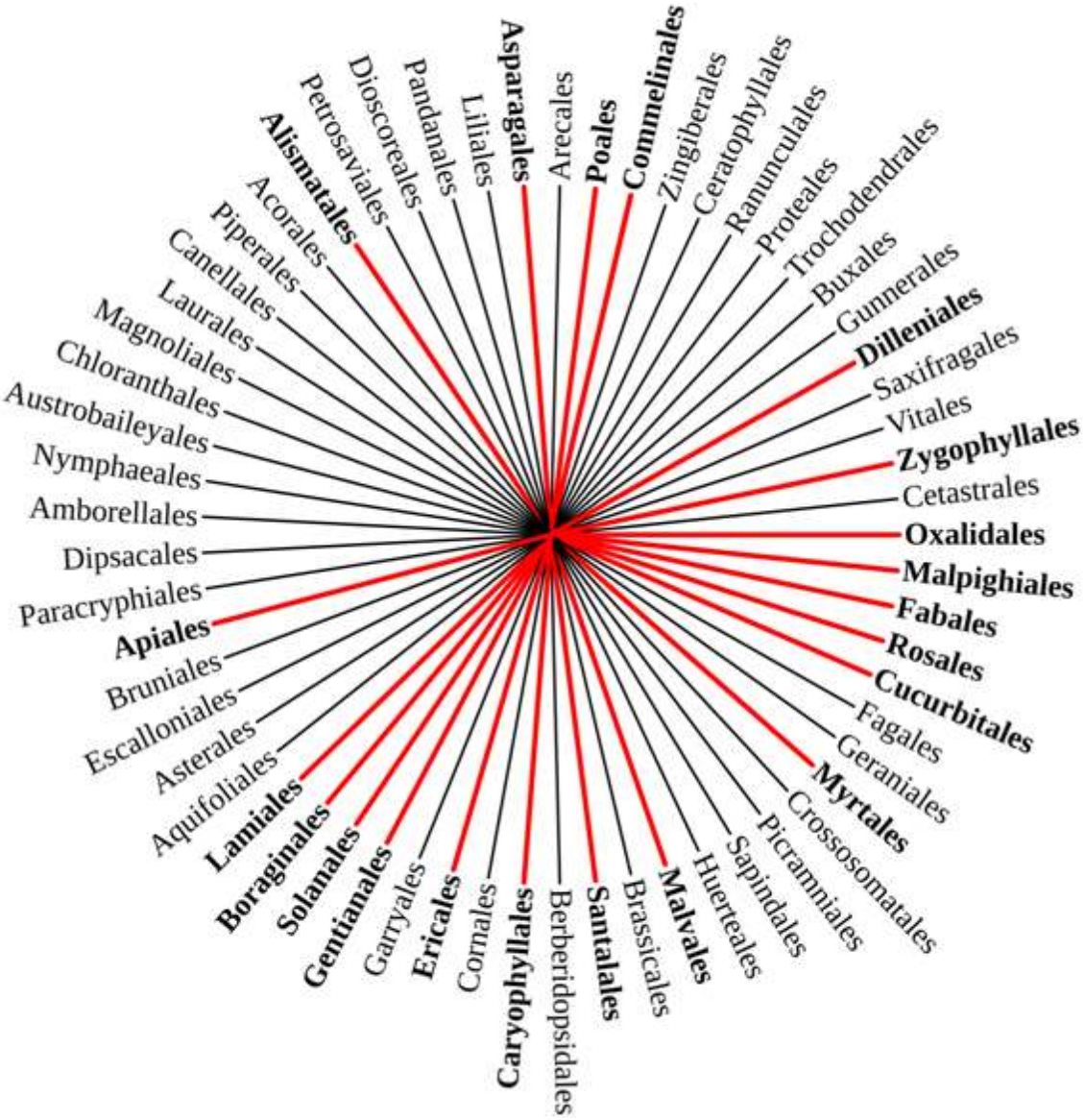


Figure 5. Phylogenetic distribution of poricidal anthers in angiosperms. Orders in bold characters and red lines indicated genera with poricidal anthers.